We thus see that many of those features which have been relied upon for the discrimination of "species" in this group are in reality but of secondary value; that, as with other corals, the characters of a *Turbinaria*, and more particularly the general form of the colony, are largely influenced by the conditions of its environment. On the other hand, *all* variation among Turbinarians (and the same is equally true of other genera) is certainly not the mere expression of adaptive modification. This is proved by the fact that specimens living side by side, and consequently under exactly the same conditions, so frequently exhibit quite obvious differences of type: such variation can only be genetic. I have myself observed, growing upon the same pearl-shell, three large Turbinarian cups which were quite typical examples of what must, in my opinion, be regarded as three distinct and well-marked species.

The question of defining the limits of a "species" is in no group such an easy one as it appears to the student who works only at the inadequate material represented in our museums*; and, in the case of the corals, it is a problem of the greatest difficulty. At every turn the zoologist who studies Nature, not merely in the museum or laboratory, but also in the field, is confronted by facts such as those to which I have alluded,—facts which bring him once more face to face with that ever-recurring question, "What is a species?"—a question to which no satisfactory answer is as yet forthcoming; to which, indeed, no satisfactory answer can be looked for until such time as taxonomic research is placed upon a more truly scientific basis—until, in short, the zoological student has at his disposal large series of specimens and other data which have been collected with the express view of aiding the solution of those problems which are summed up in that familiar word "species."

* See a recent note in 'Nature' (vol. lxiii. pp. 490–1), in which the scientific collecting of zoological material is discussed.

The Life-history of the Black-Currant Gall-mite, *Eriophyes* (*Phytoptis*) *ribis*, Westwood.

By Cecil Warburton, M.A., F.Z.S., Zoologist to the Royal Agricultural Society of England, and Alice L. Embleton, B.Sc., 1851 Exhibition Science Research Scholar, Associate of the University of Wales (Cardiff College).

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(Plates 33 & 34.)

The Black-Currant plant disease due to *Eriophyes ribis* first attracted attention in England in the year 1869, though the cause was not at first clearly ascertained. Since that time it has been the subject of frequent references by economic entomologists, who have generally recorded the fact that the pest was on the increase. To this day, however, our knowledge of the life-history of the mite is extremely limited, and the statements of various observers with regard to it are either too vague and general to be of much practical value, or are absolutely inconsistent and conflicting. No complete account of its life-cycle has yet been attempted, and its methods of distribution have remained a matter of conjecture.

The difficulty of the research is, of course, largely due to the minute size of the mite, which rarely exceeds one hundredth of an inch in length *. To observe and record the condition of the mites inside the buds at various seasons of the year is a tolerably simple matter, but a thorough investigation of their habits involved watching the creatures throughout their wanderings, and here their small size proved a serious obstacle.

In a paper on "Insects affecting the Orange" †, H. G. Hulbard described certain phenomena with regard to an allied mite which suggested to him that it owed its distribution largely to the aid of various insects and arachnids, and it was the clue thus afforded by him that was immediately responsible for the observations on distribution in the present investigation.

* The measurements are:—♀, length ·23 mm., breadth ·04 mm.
♂, „ ·16 „ ·03

† U.S. Dep. Agric. Ent. 1885.

The Eriophyidæ.

The Eriophyidæ (Phytoptidæ) or gall-mites are vermiform Acari, possessing only two pairs of legs, which have no claws, but are furnished with bristles and "feather-hairs" (Pl. 33. fig. 8; Pl. 34. figs. 10, 11). The elongated body is transversely striated, and terminates in a muscular disc-like organ (Pl. 33. fig. 9; Pl. 34. figs. 12, 13). It also presents certain bristles, of which the most important are a pair proceeding dorso-laterally from above the tail-disc.

About two hundred species of gall-mites have been described. They are all of small size, and are vegetable feeders, usually causing the abnormal growths known as galls on the leaves or stems of the plants they infest.

The Black-Currant Disease.

The disease is easily recognized by the presence, on infested bushes, of swollen and distorted buds, which, if still green, are found on examination to contain large numbers of the parasite. Badly attacked buds are entirely abortive, and eventually remain on the stems as brown dry knobs from which no leaves have arisen (Pl. 33. fig. 1). In milder cases of attack sufficient vigour is retained to give forth an enfeebled shoot (Pl. 33. fig. 2). As the hold of the disease upon the plant increases the effect becomes very striking. The failure of a large number of the buds forces into premature development the buds which would normally burst forth the following year, making overdrafts, so to speak, on the plant's vitality, and a stage is reached when it is no longer able to respond to the excessive calls made upon it. The provision for next year's foliage is already exhausted and the plant dies.

Life-history of the Mite.

The observations here recorded began on May 20, 1901, and were carried on without intermission until the middle of October. On May 20, of last year's mite-infested buds, those of which the growth had been entirely arrested were in some cases cracked, mites being visible externally in the fissures.

Individuals were also found wandering on the stems. Clearly the migration from the abortive buds had only recently commenced. Mites have been recorded by Newstead and others as wandering on the plants much earlier in the spring. It is

probable that these early wanderers are nearly all doomed to destruction, but their presence is easily accounted for. Many of the infested buds are not too much injured to put forth leaves however weakly (Pl. 33. fig. 2); and if they succeed in doing this, the mites are deprived of their shelter and rendered homeless before the formation of next year's buds. This compulsory quitting of buds of which the mite has not succeeded in entirely destroying the germinating power may be regarded as more or less fortuitous, and is a very different matter from the definite migration which appears to take place from the wholly abortive buds.

As we have seen, this commenced, in 1901, about the middle of May. The activity of the mites attained its maximum about May 30, and practically ceased about the middle of June, by which time the arrested buds were dried up and destitute of living mites.

A very careful investigation of the behaviour of the mites during this migration period revealed some interesting habits which have hitherto escaped observation.

Three different methods of locomotion are employed by these creatures in their search after new feeding-grounds. These are: (1) crawling, (2) adherence to passing insects, and (3) leaping.

Crawling.

The extremely anterior situation of the four short legs would seem to be ill-adapted for locomotion. Nevertheless the mite can crawl along quite actively, at the rate of three or four millimetres, or twelve to fifteen times its own length, a minute.

The motion of the legs is very scrambling and haphazard in appearance, but by wild exertion they drag the unwieldy body forward—an inert mass, trailing in the rear. When, however, the mite desires to change its direction, or to surmount an obstacle, the tail apparatus, with its muscular disc and bristles, comes into play. By this apparatus a hold is obtained upon the surface over which the mite is crawling, and the body is swung round, or the anterior portion is reared up and the obstacle surmounted. The tail-bristles are stronger and less wavy than they are represented in most figures of the mite, and appear to be accessory motile organs of no slight importance.

Their position in crawling may be seen in figs. 7, 20.

Distribution by Insects.

When the mites were first observed on the outside of the abortive buds, one curious point in their behaviour attracted attention, even under the slight magnification of a pocket-lens. Though some were actively crawling about, others appeared to be standing on end, and motionless, except for the waving of their legs. A series of observations and experiments were undertaken with a view to ascertaining the precise nature and purpose of this phenomenon, with the following results :—

A migrating mite, after crawling for a short distance in the manner already described, would obtain a firmer hold upon the surface of the bud with its tail-disc and assume an upright attitude (Pl. 33. figs. 5, 6, 9, Pl. 34. figs. 14, 15). The necessary hold was not always gained at the first attempt, the disc sometimes slipping, and here again the tail-bristles came into play, serving to anchor the animal to the bud and to give a certain amount of prop-like support to its rigid body. The position was not necessarily vertical, but at right angles to the supporting surface, and frequently oblique or even horizontal, and it was remarkable how the vermiform, soft-bodied mite would maintain for several minutes an attitude apparently so ill adapted to its structure. All the time its four short legs would be waving wildly in the air. A number of mites standing up in this way bore a remarkable resemblance to diminutive Hydras with greatly retracted tentacles.

After indulging in this performance for a period varying from one to five minutes, the mite would generally relax its rigid attitude, bring down its feet to the surface again, and continue its progress by crawling, only to resume its upright position and grotesque waving of legs a little farther on.

This behaviour was highly suggestive of a desire, on the part of the mite, to attach itself to any passing object, and its readiness to do so was easily proved in the most conclusive manner. If touched with a needle-point, it immediately let go its hold on the bud and was carried off on the needle. A camel's-hair brush or a feather applied to an infested bud was found to be swarming with mites on subsequent examination. In nature, the most likely carriers of the mites would, of course, be insects or arachnids. Accordingly spiders and insects of various kinds were either induced to run over infested buds, or examined after having been observed to come into contact with them spon-

taneously, and in almost every instance mites were found attached to their bodies or appendages. The fact was recorded of four different species of spider, of the larva of the currant-moth (*Abraxas grossulariata*), of the currant *Aphis*, of the larva of the two-spot ladybird (*Coccinella bipunctata*), of the black ant (*Lasius niger*), and of various other insects. So uniform was the result, that the investigation into the various creatures capable of distributing the mite was presently discontinued, as it was clear that almost any insect might perform that function, though those which wander widely and especially affect currant-bushes would necessarily be most efficient. It is probable that the currant *Aphis* is especially instrumental in spreading the disease. It crawls slowly along, feeling its way with its antennæ, to which the mites readily attach themselves, and the winged individuals would be extremely likely to convey the pest direct to another currant-bush.

Method of Attachment.

The mites do not seem in any true sense to grasp the objects presented to them, nor, indeed, do they possess any prehensile organ, unless the tail-disc may be placed in that category. Moreover, ordinary hairs and bristles are much too thick, relatively to the mites, for seizure by means of the jaws or legs.

Attachment always seems to take place, in the first instance, simply on account of some adhesive substance with which the bodies of the animals are coated.

A mite may be removed by any portion of its body being touched by the antenna of an aphis, but it quickly coils itself round the appendage in a worm-like fashion and brings its tail-disc into play.

Possibly the bristles and "feather-hairs" (Pl. 33. fig. 8) on the legs of the mite may to some degree entangle themselves among the fine hairs on the bodies and legs of insects. When removed on a camel's-hair brush the mites wriggle in and out among the hairs and soon secure a tolerably firm hold.

Leaping.

While the behaviour of the upright mites was under observation under the microscope, it was noticed that individuals sometimes disappeared from the field of view with a suddenness that made it impossible to see what precisely had happened. This

occurred several times before it was realized that the disappearance was not accidental, but that the animals were, in fact, leaping.

As soon as this was suspected, it was easy to verify it by concentrating attention on one individual and using powers which allowed the whole of its flight to be followed. The conclusions arrived at were these:—After several vain attempts to attach itself to a passing insect, a mite would cease to wave its legs, remain rigid a moment, and then launch itself forth, torpedo-like, into space. The precise mechanism by which this was effected could not be determined, but the terminal muscular disc, which had been observed to be retractile, was evidently the propelling organ. The tail-bristles were at first suspected of taking some part in the action, but further observation showed that, by retaining too firm a hold on the bud, they sometimes rendered the leap abortive, the mite simply falling backwards with considerable impetus instead of darting away. No great distance was covered by the leap, the longest measured being four millimetres, or about sixteen times the animal's length. When the mites leaped from a bud placed on a microscope-slide they alighted on their heads and fell over with the tail-disc most distant from the point of departure.

It was an interesting and suggestive fact that while the mites would remain upright with waving legs for several minutes in the still air of the laboratory, they could be induced to leap at once by blowing upon them with the breath or by means of a pipette. It would seem, then, that they first of all try to come in contact with a passing insect, and, failing this, take advantage of a puff of air to attain their object.

In view of the extremely doubtful advantage of a blind leap into space, the conjecture may be hazarded that the mite thus sometimes attains a flying insect which hovers near enough to fan it by the beating of its wings.

Destination of the Migrating Mites.

The problem of the immediate object of the mites in leaving the old buds by crawling, leaping, and adhering to insects next demanded a solution. At the height of the migration the new buds were already visible and beginning to swell, and the manner in which and the extent to which they acquired the disease had still to be ascertained. Moreover, the leap into space would

necessarily land many of the creatures on the ground, and it was conceivable that they sought or made some kind of shelter there from which a new attack sprang at a later period, or even that they sought the roots and set up there another form of the infestation. Finally, as it transpired that here and there a resting-bud which had begun to show after the conclusion of the migratory period contained the mites, it seemed possible that some might find a temporary shelter under the loose bark of the stem in the neighbourhood of such buds while still undeveloped. All these points were subject to careful investigation, the results of which may now be stated.

Shelter under Bark.

Unless called upon to furnish shoots on account of the extensive destruction of the ordinary buds by disease or injury, the resting-buds remain as almost invisible knobs under the bark of the stem. There is usually some loose bark in their vicinity and this was carefully searched for the mite, but with uniformly negative results. Specimens of a *Tyroglyphus* were found, and also some empty and longitudinally split shells which might have been hypopal casts, but of the gall-mite not a specimen.

Behaviour on the Ground.

To trace the actions of such minute creatures amongst the precipices and chasms into which ordinary soil is converted by the microscope is well-nigh impossible. By preparing a specially fine mould the difficulty was reduced, and it was hoped that any tendency to burrow into the earth or to encyst in sheltered recesses would at all events be detected. Experiments were made with both wet and dry earth, but here again the results were entirely negative. The mites showed no indication of having attained a desired end, but crawled laboriously among the particles of earth, rearing themselves at intervals and waving their legs as though in the hope of rescue at the eleventh hour by some passing insect No burrowing, no encystment, no deposition of eggs was noted. For hours, even for days, the mites wandered aimlessly, becoming less and less vigorous till at length they died. On the dry mould they were more active at first, as the wet soil seemed to have a paralyzing effect for the time being. In the latter case the mites, however, lived the longer, several showing signs of life after the third day.

Further experiments were made with black-currant roots which were placed upon the soil and dusted with actively migrating mites. Again nothing definite happened, the mites seemed in no way contented with their new environment, and acted as though the object of their migration were as far from attainment as ever. Such negative results are, of course, inconclusive, but it seems likely that all the mites which fall to the ground are doomed to perish unless they should have the extreme good fortune to be carried by some passing insect to another bush.

Entry into the new Buds.

During the first week in June the mites were wandering actively about the stems, and some were found in the axils of the leaves, and close to and upon the new buds (Pl. 33. figs. 3, 4). On June 7 a mite artificially placed upon a young bud was seen to work its way in between the sheathing-leaves. New buds were removed at frequent intervals and examined for mites, which were found inside for the first time on June 8. During the ten days of more or less active migration which succeeded, the search for mites was successful in a fair percentage of cases, but from the number of buds which afterwards proved to be diseased it is likely that the presence of one or two of the animals was frequently overlooked—a fact, perhaps, not greatly to be wondered at. The mites in any one bud were always extremely few in number. Till June 12 the weather had been hot and dry, and on that date very few mites were wandering, and those still within the old diseased buds showed slight signs of life. The migration was apparently almost at an end. Rain then fell, and this seemed to revive many of the mites and to prolong the migration period for a few days. With rare exceptions, wandering mites were not seen after June 19, by which time the old abortive buds were entirely lifeless. The migration, therefore, was at an end, and of the hosts of mites in existence at the end of May an infinitesimal number had obtained a footing in the new buds, all the rest having presumably perished.

Behaviour of the Mites within the young Buds.

The migrating mites were for the most part adult, and eggs could be seen in the transparent bodies of the females (Pl. 33. fig. 7). The date of the deposition of these eggs seemed to be a matter of some importance, though by no means easy to ascertain. The plan of searching for them by the dissection of individual buds was abandoned, but new buds were daily removed from

infested bushes, cut into small fragments, and placed in tubes of spirit. These were shaken vigorously and then allowed to stand, and the sediment examined under the microscope.

Eggs were first found in the buds removed on June 26. After that date they occurred in increasing numbers. By the end of the first week of July the new attack appeared to be firmly established. Mites in all stages of development, as well as eggs, could easily be found by dissection of the new buds, some of which seemed to show signs of abnormal development. In every case the mites were centrally situated in the buds—a remarkable fact in view of their particularly compact structure in this plant, which would render it by no means easy for the immigrant mites to reach the interior.

As the brood increased, the mites worked centrifugally, encroaching gradually upon the more external portions of the bud.

By July 20 the removal of two outside leaves sufficed, in some cases, to reveal the mites, and by the end of the month they were almost external in the most advanced buds, covered only by the loosely applied outermost leaves, while occasionally one or two individuals were found actually on the outside of the buds.

The multiplication of the mites in the new buds had been so rapid during July and August, that it appeared highly probable that a second migration period was approaching. None such, however, was observed. The buds continued to swell, but remained green, and did not burst, and no wandering mites were detected during the autumn. The creatures were now established in their winter-quarters and were reproducing less actively. No new fact was to be added to the record of their life-history. Some might succumb to the rigours of winter, but the survivors would be ready to recommence the life-cycle in the following spring.

Animals associated with the Mite.

Running with great activity over the twigs of infested bushes, examples of a red mite of the genus *Actineda* were constantly found. No conclusive evidence of its habits was obtained, but one specimen had attached to its jaws what appeared to be empty *Eriophyes*-skins, and it is quite possible that it preys to some extent on the mite, for it belongs to a predaceous group of the Trombidiidæ.

Within the diseased buds specimens of a *Tyroglyphus* mite were

very frequently observed, and on one occasion, in October, a species of *Tarsonemus* was found. These are vegetable feeders, and could not have been preying upon the *Eriophyes*.

In a large proportion of the mite-infested buds dissection revealed the presence of a small dipterous larva, apparently that of a Cecidomyid fly (Pl. 34. figs. 21, 22). It was hoped that some examples would be reared and the imago obtained and identified, but its development is so slow that larvæ observed in October are little larger than those seen in July, and show no signs of pupation. Probably the fly will not emerge until next spring, when it is quite likely to prove a new species. It is always found at, or near, the centre of the bud, and feeds upon the mites. Its slow growth probably implies a moderation of appetite which allows the mites, by their extreme fertility, to renew their numbers as fast as they are depleted, and thus to keep up the food-supply.

The Red-Currant Plant and the Mite.

As none of the characteristic swollen buds appeared on red-currant bushes, which, moreover, flourished in the immediate neighbourhood of failing black-currant plants, it was believed that the red-currant was practically immune. When the Cecidomyid larva above mentioned was first observed and some doubt was entertained as to its habits, red-currant buds were examined to see if they contained the grub, the inference being that the presence of the grub would show that it fed upon the bud and not on the mite.

The result of the examination was entirely unexpected, for the *mites* were found in considerable numbers. The attack differed remarkably from that on the black-currant, the infestation working from the outside inwards. At first they were only found in the axils of the leaves at the base of the buds, and perhaps within the first brown sheathing-leaves. Later they penetrated more deeply and had almost reached the centre.

That they were not merely sheltering there but were obtaining nourishment was proved by the presence of eggs and larvæ. No great harm, however, seemed to be done by them, nor were they ever found except on bushes near to badly attacked black-currant plants.

Conclusions.

The observations above recorded may be thus briefly summarized :—

1. Of the mites surviving the winter, those which have not succeeded in entirely arresting the growth of the buds, but are driven out by their development before May, probably perish.

2. There is a definite migration period, which takes place as the abortive buds dry up and become uninhabitable, the new buds being then ready for the reception of the mites. In 1901 this period extended from the middle of May to the middle of June. Any mites found wandering in the autumn are probably of the nature of an overflow.

3. Distribution is effected by (1) crawling, (2) adhering to insects, (3) leaping.

4. *There is a brief period when the total number of living mites is exceedingly few, the old buds being dead, while the emigrants which have attained the new buds have not yet increased to any considerable extent. This period in 1901 coincided with the last week in June.*

5. The mites are unable to maintain life in the ground, nor do they attack the roots.

6. The red-currant plant can contract the disease, but does not appear to suffer greatly from it. The mites first appear on the outside of the buds, penetrating inwards as they increase in number.

7. Infested buds very commonly contain a Cecidomyid larva which feeds on the mites.

If the results thus obtained are trustworthy, certain inferences follow with regard to the treatment of the disease. The most important are these :—

1. Any treatment of the ground under infested bushes is unnecessary, as the mites do not live in the soil.

2. Spraying in the early spring is only calculated to destroy mites which would perish in any case.

3. The only time when spraying would be likely to prove beneficial is at the end of May and the beginning of June, when it is undesirable on account of the blossom.

4. The removal of all the new shoots from infested bushes at the end of June, if practicable, would apparently clear the plants of the disease. It is at all events important to remember that at this time the pest is reduced to a minimum.